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## The limits of the Araneoidea (Arachnida : Araneae)

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### Abstract

A comparative morphological study of the following spider families is presented: Anapidae, Micropholcommatidae, Tetracellidae, Mimidae, Malkaridae, Archaeidae and Pararchaeidae. The results provide strong evidence for the placement of Tetracellidae and Micropholcommatidae in the Araneoidea. Among others, probably the best autapomorphic character for the Araneoidea, the triad (three spigots together producing the gluey capture thread) could be found in all six species of micropholcommatids and tetracellids in both females and males. Within the Araneoidea, these two families share many characters with the Anapidae, thus their assignment to the higher symphytognathoids is most likely to be correct. The presence of a labral spur in the Micropholcommatidae is also verified.

Mimidae and Malkaridae are most probably araneoid. The position and monophyly of the Archaeidae *s.l.* remains doubtful.

The Palpimanoidea, which was considerably enlarged in a revision by Forster and Platnick (1984), is therefore here cut back to its original size.

### Introduction

The superfamily Araneoidea currently comprises 12 families the relationships of which have recently been analysed by Griswold *et al.* (1998). About 10 000 species of Araneoidea have been described and many more await discovery. With only a few exceptions, all spiders currently assigned to the Araneoidea are known to build webs with very diverse architecture. Among them the best known and most admired web construction is the orb of the Araneidae.

The most convincing definition of the Araneoidea was proposed by Coddington (1986): spiders that are able to produce gluey capture threads. This behavioural feature corresponds with a morphological structure, the triad. A triad is a functional unit consisting of three silk glands, which leads into each posterior lateral spinneret (Peters 1955). Other suggested autapomorphies that support the taxon Araneoidea are the structure of the male palpus, especially the presence of a paracymbium (e.g. Lehtinen 1967; Coddington 1986), as well as the ultrastructure of the leg cuticle and setae (Lehtinen 1996).

The only author to doubt the monophyly of the Araneoidea was Millidge (1988), who suggested that the closest relatives of the Linyphiidae are the Agelenidae and other sheet-web builders, and that the Linyphiidae should be removed from the Araneoidea. Peters and Kooor's (1991) thorough investigations showed that Millidge's conclusions were based on incorrect facts. Thus, the monophyly of the superfamily Araneoidea is undoubted, but not its limits. Four families previously placed in the Araneoidea (Mimidae, Micropholcommatidae, Tetracellidae, and Archaeidae) were transferred to the Palpimanoidea by Forster and Platnick (1984); the Archaeidae were at the same time split into four families: Archaeidae *s.str.*, Mecysmaucheniidae, and the two monogeneric families Holarchaeidae and Pararchaeidae. This revision meant a considerable enlargement of the taxon Palpimanoidea, which had comprised until then the Palpimanidae, the Stenochilidae and the Huttoniidae.

Two cheliceral characters were proposed as autapomorphies for the new large superfamily Palpimanoidea by Forster and Platnick (1984): the presence of peg teeth (modified setae) on the promargin of the cheliceral furrow, and the presence of an elevation that is punctured by presumptively glandular pores. The occurrence of peg teeth in other unrelated Araneomorphae were regarded as convergent features.

The monophyly of the Palpimanoidea was doubted by many arachnologists (e.g. Wunderlich 1986; Lehtinen 1996) but adopted by others (Coddington and Levi 1991). The removal of the transferred families made the Araneoidea a more conveniently manageable group of web-building spiders. But even Platnick and Shadab (1993) admitted that 'the cheliceral characters are not ideal'. In fact, both autapomorphies can also be found in some araneoid spiders (Heimer and Nentwig 1982; Platnick and Shadab 1993). One of the main arguments for the family transfer was that these newly placed taxa lack a triad (Coddington and Levi 1991; Platnick and Shadab 1993). However, the only hitherto known documentation of spinneret morphology in the Tetracellidae (Platnick *et al.* 1991: figs 241, 242, 244) is ambiguous, i.e. it is not clearly discernible whether a triad is present or not.

The superfamilial placement of the Mimetidae has been particularly disputed. On the one hand they show the typical overall appearance of araneoid spiders and the male has a pedipalp that resembles the araneoid pattern and not just in showing a paracymbium (Shear 1981), whereas, on the other hand, they have distinct peg teeth even though they lack clearly developed gland mounds (Forster and Platnick 1984). The fact that the Mimetidae are distributed world-wide and are well-known spiders might be one reason for the vehemence of the dispute. Another reason is that their removal from the Palpimanoidea would leave only one very weak apomorphic character (the reduction of leg spination) to justify the group, and thus would result in the collapse of the superfamily.

*Malkara*, a new genus described by Davies (1980) as a subfamily of Araneidae, also has a paracymbium. Wunderlich (1986) elevated the taxon to its own family and placed the Malkaridae as sister-group of Mimetidae on the basis of similarities in the spination of the first two pairs of legs. Platnick and Forster (1987) supposed that it could also be a highly derived subgroup of Mimetidae. This is just one of a series of examples of taxa that were shifted between the Mimetidae and the Araneidae (Heimer 1984; Platnick and Shadab 1993).

The superfamilial placement of the small tropical spider families Micropholcommatidae and Tetracellidae are much less controversial, although they are the only web-builders among the Palpimanoidea (Hickman 1945; Forster 1959). Both families were established by Hickman (1944, 1945) for tiny moss-dwelling spiders from the Australasian region. Much later they were also recorded from South America (Forster and Platnick 1981; Platnick and Forster 1986). Forster (1959) transferred the Micropholcommatidae and Tetracellidae to the Symphytognathidae, which was also established by Hickman (1931) for a Tasmanian spider. The Symphytognathidae *sensu* Forster (1959) included the current families Anapidae, Micropholcommatidae, Mysmenidae, Symphytognathidae and Tetracellidae (Forster and Platnick 1977). It is this taxon that will be re-established in this study on the basis of morphological features.

Griswold *et al.* (1998) added the Theridiosomatidae to their symphytognathoids. With that, spiders with a distinct paracymbium were included for the first time.

## Material and Methods

### *Investigated species*

A list of the species examined for this study is given in Table 1.

### *Morphology*

The specimens were dehydrated in acetone, dried with the critical-point method or with hexamethyldisilazane (HMDS), mounted with nail varnish, sputter-coated with gold, and examined with a scanning electron microscope (JEOL JSM-6400). As far as possible, the spinnerets were cleaned by means of a thin jet of alcohol produced by a syringe. The spinnerets of the fresh material (mimetids only) were spread out by carefully squeezing the abdomen. The use of nail varnish as glue to secure the preparations is especially advantageous for rare spider material, because the specimens can easily be removed from the stubs with the help of a dissecting needle, glued on in another position, sputter-coated a second time, and examined from a new perspective. Only some bristles become lost during this procedure.

**Table 1. Details of material examined for this study**

The specimens were gifts from the following individuals or institutions: AMSA = Australian Museum, Sydney, Australia; CK = Christian Kropf, Bern, Switzerland; ZMB= Zoologisches Museum, Berlin, Germany; QMBA = Queensland Museum, South Brisbane, Australia; RF = Ray Forster, Dunedin, New Zealand; JW = Jörg Wunderlich, Straubenhard, Germany

Families and species	Sex and stage	Origins	Collectors	Donors
Anapidae:				
<i>Comaroma simoni</i> Bertkau, 1889	♀, ♂	Austria	Kropf	CK
? <i>Dippenaaria</i> sp. <sup>A</sup>	♀, ♂, subadults	South Africa	Uhlig	ZMB
<i>Pseudanapis hoeferi</i> Kropf, 1995	♀, ♂	Brazil	Kropf	CK
Archaeidae:				
<i>Archaea</i> sp.	♀	Madagascar	Emerit	JW
Malkaridae:				
<i>Malkara loricata</i> Davies, 1980	♀, ♂, subadult, juvenile	Australia	Davies/Raven	QMBA
Micropholcommatidae:				
<i>Micropholcomma parmatum</i> Hickman, 1943	♀, ♂	Tasmania	Hickman	JW
<i>Micropholcomma</i> sp.	♀, ♂	Australia	Gray	AMSA
<i>Parapua punctata</i> Forster, 1959	♀	New Zealand	Forster	RF
Mimetidae:				
<i>Ero aphana</i> (Walckenaer, 1802)	juvenile	France	Schütt	—
<i>Ero cambridgei</i> Kulczynski, 1911	♀, ♂	Germany	Schütt	—
<i>Ero furcata</i> (Villers, 1789)	♀, ♂	Germany	Schütt	—
<i>Ero</i> sp.	first instar	Germany	Schütt	—
Pararchaeidae:				
<i>Pararchaea bryophila</i> Hickman, 1969	♀, ♂	Tasmania	Hickman	JW
Textricellidae:				
<i>Textricella vulgaris</i> Forster, 1959	♀, ♂	New Zealand	Forster	RF
<i>Textricella fulva</i> Hickman, 1945	♀, ♂	Tasmania	Hickman	JW
<i>Textricella parva</i> Hickman, 1945	♀, ♂	Tasmania	Hickman	JW

<sup>A</sup>?*Dippenaaria* sp. is an undescribed species from South Africa that is closely related to *Dippenaaria* and *Anapisona* (Wunderlich, personal communication).

### Conventions

Platnick and Forster (1986) synonymised Textricellidae with Micropholcommatidae since they could not clearly assign *Teutoniella* to one of these families. In this paper, I still use both family names because the six investigated taxa can be subdivided into two distinct groups on the basis of the absence or presence of the anterior median eyes, the female palp, and spinneret morphology (see below). All three taxa (Micropholcommatidae, Textricellidae and Anapidae) are hard to delimit from each other and are therefore used as working hypotheses here.

Actually, the term Anapidae *s.l.* should have had priority over Symphytognathidae *s.l.* since the name Anapidae can be traced back to Anapeae Simon 1895 (see also Kraus 1967). I still use Symphytognathidae *s.l.* for the sake of better communication.

Forster and Platnick (1984) kept the name Palpimanoidea for the enlarged superfamily, although Archeoidea (based on an older family name) would have been the correct name according to the rules of nomenclature. However, in order to avoid misunderstanding I will use the name 'Palpimanoidea' in the sense of Forster and Platnick (1984), since it has become well established.

## Results

### Size

The Micropholcommatidae, Textricellidae and Anapidae, as well as *Pararchaea* examined in this study are relatively short-legged, minute spiders with a body length of 0.8–1.6 mm. Although still rather small, the Archaeidae, Mimetidae and Malkaridae are considerably larger.

### Scutae

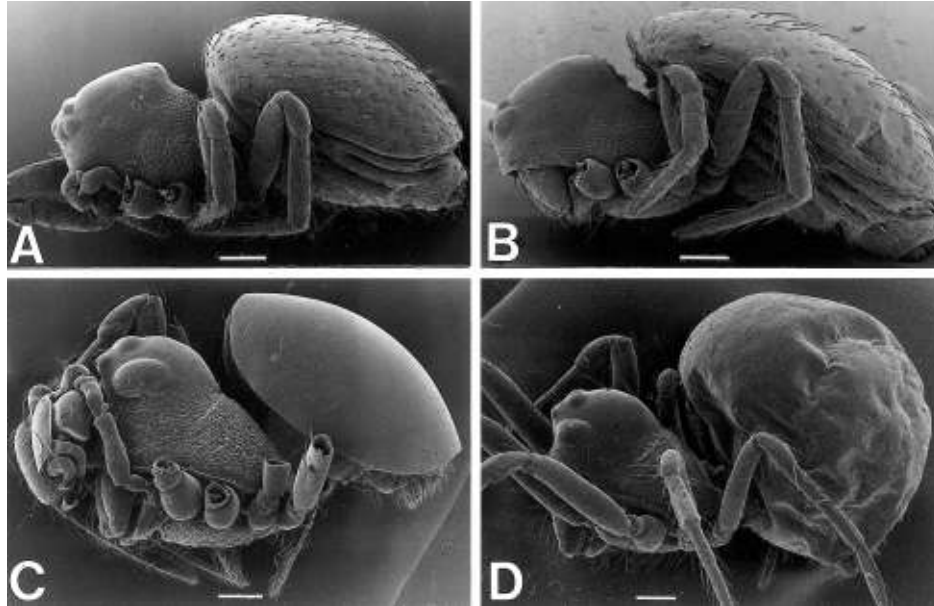
Many of the spiders included in this study show a strengthening of the abdominal cuticle in the same typical pattern: the dorsal surface of the abdomen is entirely, or almost entirely, covered by a scutum, the ventral surface bears two rings, one of which encircles the spinnerets, the other the pedicel. The pedicel ring is sometimes enlarged and covers the epigastric region as well. The dorsal thickening of the cuticle is, in some spiders, as hard as the surface of an oribatid mite (male anapids, Fig. 1C) or just coriaceous in other spiders (*Pararchaea*, *Malkara*, textricellids, micropholcommatids, Fig. 1A, B). In the latter the strengthening is present in both sexes, whereas in the anapids the females can differ from the males in lacking the dorsal scutum (?*Dippenaaria*, Fig. 1D).

### Carapace and eyes

The outline of the carapace varies widely within the studied species. Some carapaces are flat, as in *Malkara*, whereas others are characterised by elevations. Most striking are the extremely high raised *pars cephalica* of the archaeid spiders (Fig. 2G). The highest point of the carapace is situated in the posterior half in the Mimetidae, Pararchaeidae, Micropholcommatidae and Textricellidae (Fig. 2B–E). In anapids the anterior half is raised, with the highest point a short distance behind the eye region (Fig. 2A). A pore-bearing depression situated anterolaterally on the carapace is found only in *Comaroma* but not in ?*Dippenaaria* or any of the other investigated species. In contrast to the other families, the Archaeidae and Pararchaeidae have a short clypeus (Fig. 2D, G) and the chelicerae are encircled by the anterior margin of the carapace. All studied spiders have eight eyes in two rows. The lateral eyes are contiguous. In the Anapidae and Mimetidae they even share a common elevation (Fig. 2A, E). The anterior median eyes are considerably reduced in size in the Anapidae and Textricellidae (Fig. 3A, B), and in *Micropholcomma*.

### Female palp

The female palp of the Micropholcommatidae and Anapidae are clearly reduced in size and in the number of segments (Fig. 3D–G). Only the trochanter as a vestigial remnant is left in the anapids and in *Micropholcomma* (Fig. 3D, E, G). *Parapua* has a very short female pedipalp with only three segments in addition to the coxa (Fig. 3F). All these reduced pedipalps vary in size



**Fig. 1.** Body, lateral view. A, B, *Micropholcomma parmatum* (Micropholcommatidae); C, D, *?Dippenaaria* sp. (Anapidae); A, C, males; B, D, females. Scale bars: 100  $\mu$ m.

and form among specimens and are sometimes asymmetrically developed. The palpal claw is lacking in female *Pararchaea* and in the tetracellids.

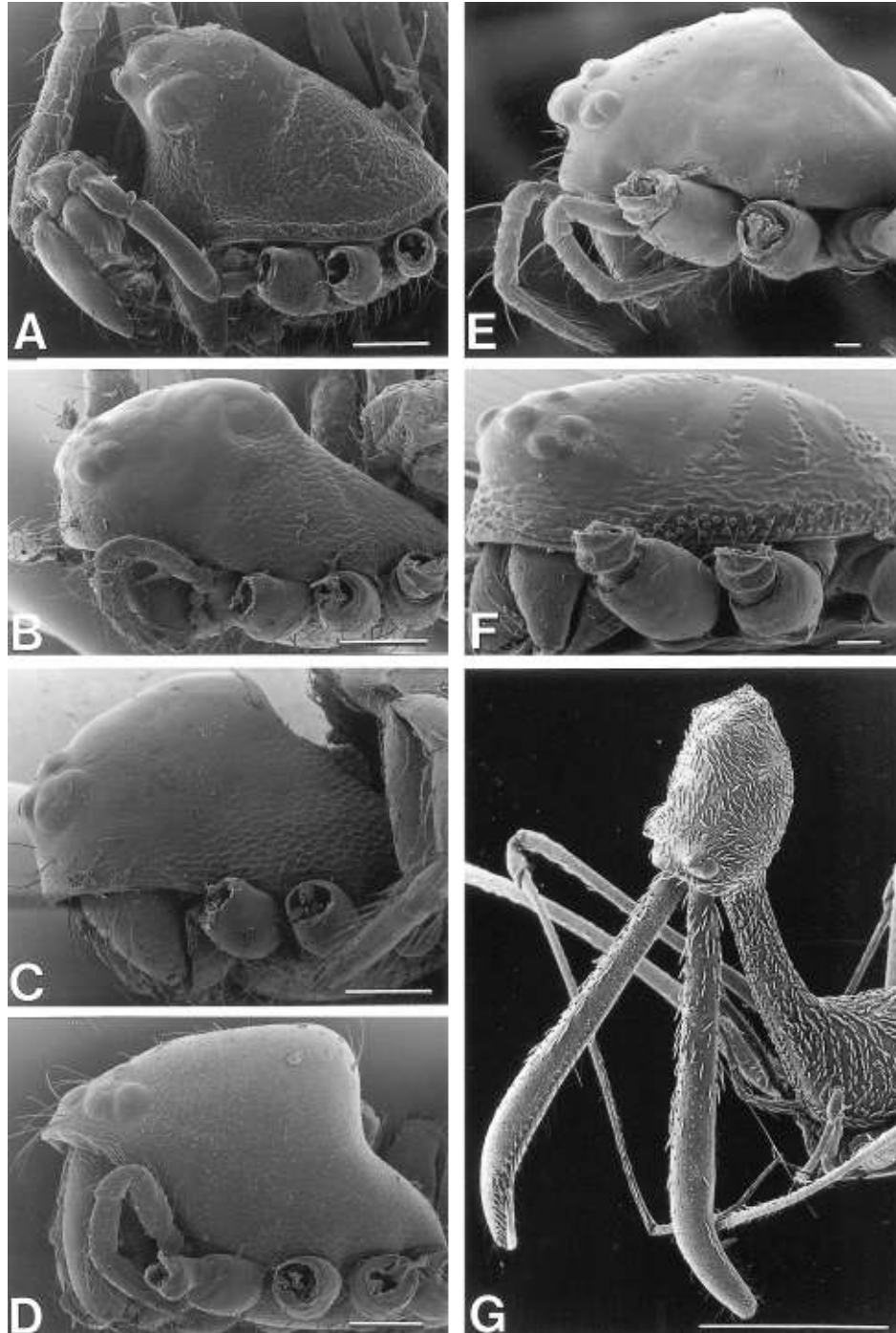
#### *Chelicerae*

Both *Archaea* and *Pararchaea* have elongated chelicerae with stridulatory ridges on the outer surface. The chelicerae of the other species examined are relatively short and stout and lack the stridulatory file. Only the extremely elongated chelicerae of the Archaeidae are splayed out so that the fangs are far apart (Fig. 2G).

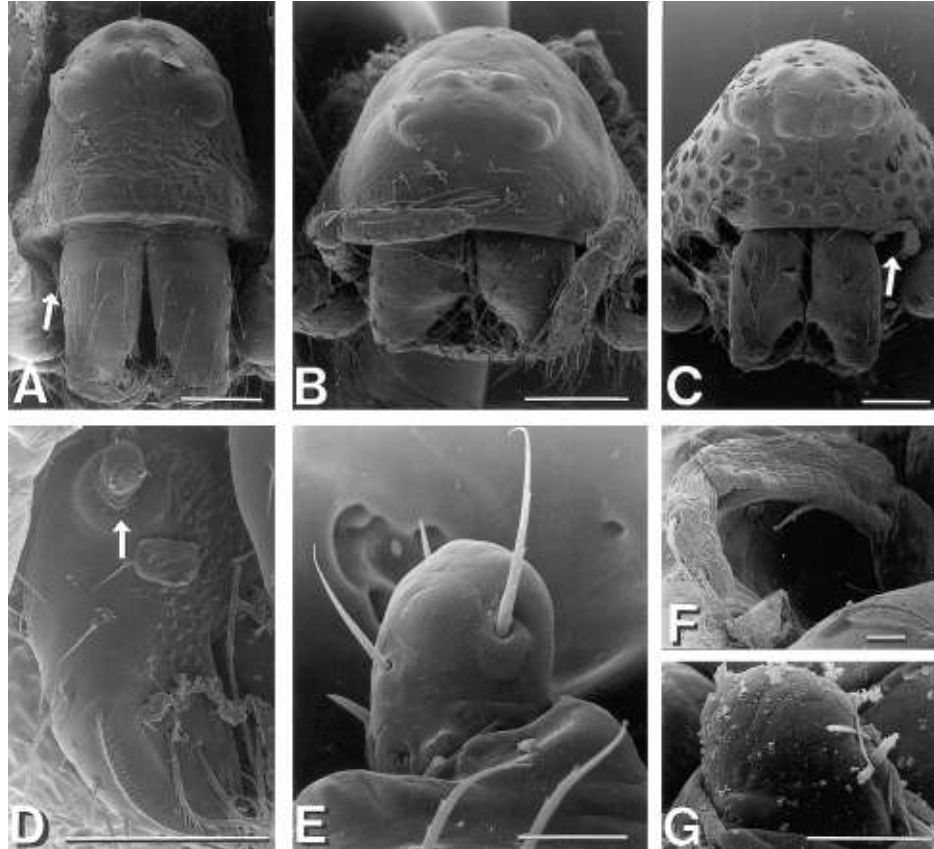
Two different types of teeth can be found along the margins of the cheliceral claw furrow. The peg teeth, which are characterised by a socket and a grooved shaft (Fig. 4B), are interpreted as modified setae (Forster and Platnick 1984) and are sometimes difficult to delimit against other short, stout setae. The second, more common type are the true teeth, which result from thorn-like elevations of the cuticle, i.e. they are not divided into a socket and a shaft (e.g. Fig. 4D). In outline, true teeth are conical or triangular and their surfaces are smooth. In some spiders cheliceral gland mounds are present. These are pore-bearing elevations situated at the inner side of the claw furrow. The function of the cheliceral gland mound is unknown.

*Archaea* has a long row of approximately 20 peg teeth along the promargin of the (weakly developed) cheliceral furrow. This row continues to the base of the chelicera but the peg teeth become successively more seta-like in appearance the closer to the base that they originate (Fig. 2G). The inner margin is flanked by one small peg tooth, a cheliceral gland mound, and three other round elevations that bear no pores but are similar to the gland mound in having grooves at the top. Two long slender setae originate at the distal base of the gland mound (Fig. 4C).

The promargin of the cheliceral furrow of *Pararchaea* shows about 10 peg teeth that are similar to those of *Archaea* except that they stand closer and their sockets are more or less fused together. The inner margin bears no teeth and no gland mound. The tip of a keel that runs along the posterior side of the chelicera could be mistaken for a normal true tooth.



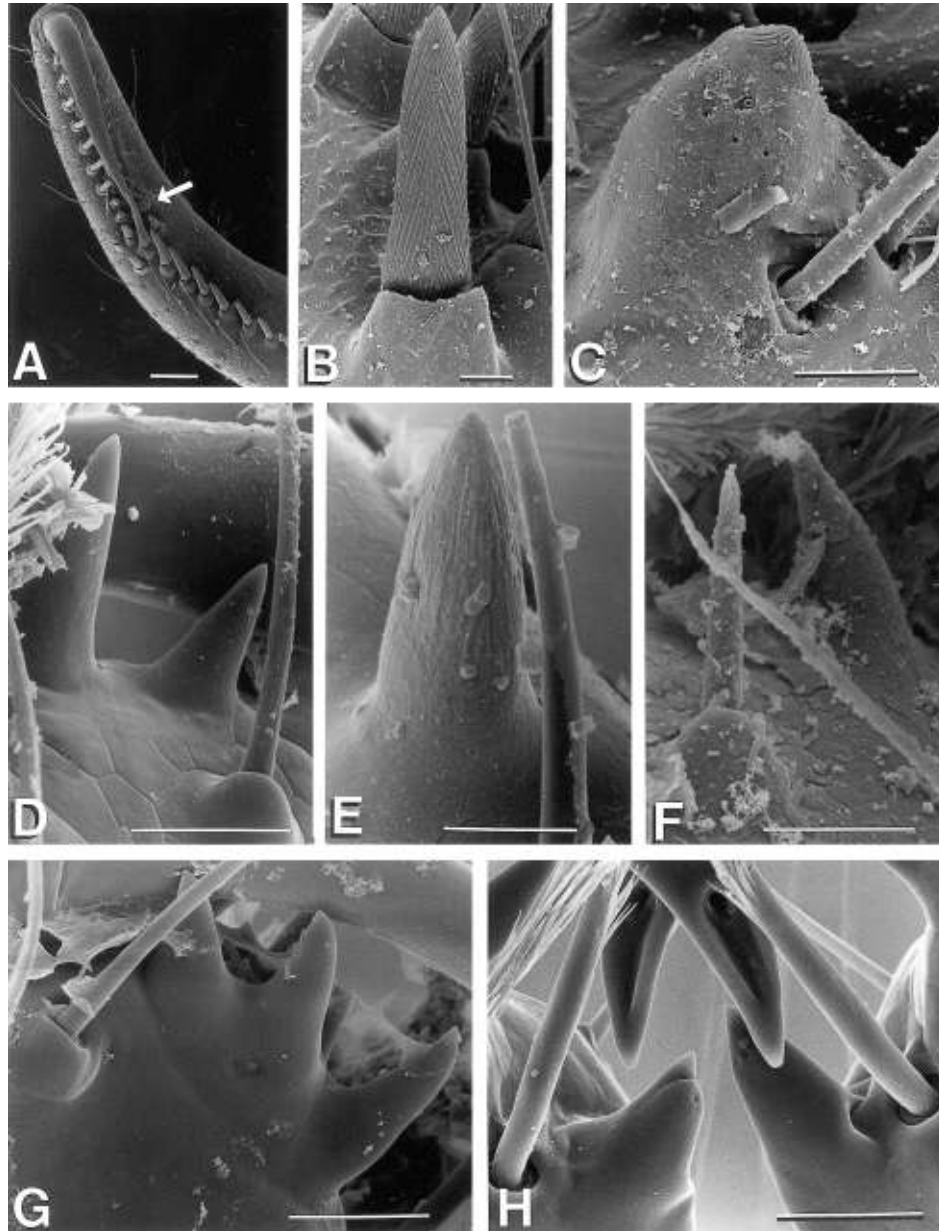
**Fig. 2.** Prosoma, lateral view. *A*, ?*Dippenaaria* sp. (Anapidae), male; *B*, *Textricella vulgaris* (Textricellidae), female; *C*, *Micropholcomma parmatum* (Micropholcommatidae), male; *D*, *Pararchaea bryophila* (Pararchaeidae), female; *E*, *Ero furcata* (Mimetidae), female; *F*, *Malkara loricata* (Malkaridae), juvenile; *G*, *Archaea* sp. (Archaeidae), female. Scale bars: 100  $\mu$ m.



**Fig. 3.** Prosoma, endite, and pedipalp of female spiders. A, D, E, *?Dippenaaria* sp. (Anapidae); B, *Textricella vulgaris* (Textricellidae); C, F, *Parapua punctata* (Micropholcommatidae); G, *Micropholcomma parmatum* (Micropholcommatidae); A–C, prosoma, frontal view, the arrows in A indicate the vestigial remnants of the pedipalps; D, endite with reduced pedipalp, frontal view with chelicerae removed; E, G, vestigial pedipalp, ventral view; F, pedipalp;. Scale bars A–C, 100  $\mu$ m; D–G, 10  $\mu$ m.

*Ero* has peg teeth along the promargin of the furrow and a smooth retromargin. Between the peg teeth stronger setae are situated, which also have a small socket and a shaft with a longitudinal structured surface. The chelicera of *Malkara* bears only two true teeth plus three setae on the promargin and one seta on the posterior surface.

The Micropholcommatidae and Textricellidae have only a very few cheliceral teeth. The furrow is bordered by two or three true teeth on the promargin and one on the retromargin. Distinct peg teeth are not present, but there is one strong seta on the anterior surface (Fig. 4D–F). A cheliceral gland mound could not be observed in the micropholcommatids; however, these structures are difficult to spot, so we cannot rule out the presence of gland mounds in these spiders. *?Dippenaaria* has true teeth only. The three distal teeth share a common elevation and so have a cockscomb-like appearance (Fig. 4G). A single, large tooth is situated exactly opposite the fang opening. This median tooth is fused with a cheliceral gland mound on its posterior side (Fig. 4H). If there is a gland mound present in textricellids, it is in the same position and has the same appearance as in anapids. The tooth triplet with the common mound is also developed in *Textricella parva*.



**Fig. 4.** Cheliceral teeth and cheliceral gland mounds. *A–C*, *Archaea* sp. (Archaeidae), female; *A*, medial view of the left chelicera, arrow indicates the gland mound; *B*, peg tooth; *C*, gland mound; *D*, *Textricella vulgaris* (Textricellidae), female, teeth and seta of the right chelicera in frontal view; *E*, *Parapua punctata* (Micropholcommatidae), female, tooth, frontal view; *F*, *Micropholcomma parmatum* (Micropholcommatidae), female, two different cheliceral teeth, frontal view; *G*, *H*, *?Dippenaaria* sp. (Anapidae), male; *G*, three teeth with common base on cheliceral promargin of the left side; *H*, gland mounds of the left and right chelicerae on the back of the true teeth, caudal view. Scale bars: *A*, 100  $\mu$ m; *B–H*, 10  $\mu$ m.

### Mouthparts

The presence of a labral spur was thought to be an apomorphic character of the Anapidae by Platnick and Shadab (1978). The ‘spur’ is an elevated sclerite that often bears a tongue-shaped appendage and is visible on the front side of the labrum (Fig. 5A–C). However, closer examinations of *Parapua* and *Micropholcomma* (Fig. 5D–F) showed that the labral spur is not unique to the Anapidae. The function of the labral spur is unknown, but it seems to possess a basal joint so that the appendage can probably be moved to project anteriorly. The labral spur is present and more or less equally developed in both sexes. It is sometimes visible between the chelicerae if they are splayed a little, but in order to examine the labra more closely it is necessary to remove the overlying chelicerae. The presence or absence of a labral spur in the Textricellidae could not be determined. In *Archaea*, the labrum is characterised by a large lobe with a pair of lateral outgrowths and a tuft of hairs on the midline.

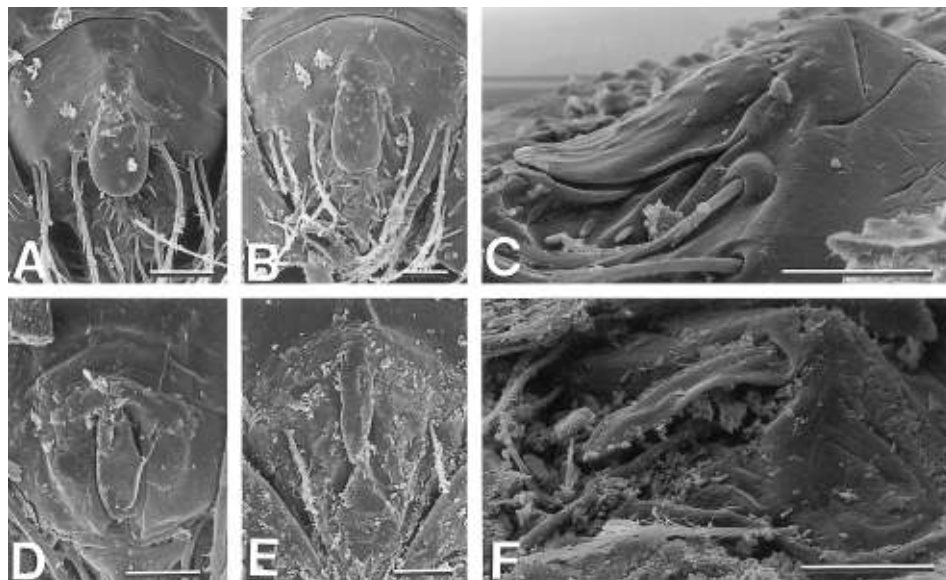
### Paracymbium

A paracymbium occurs in three families that are currently assigned to the Palpimanoidea. In both *Pararchaea* (Fig. 6C, D) and *Malkara* (Fig. 6A) the paracymbium is a basal hook-shaped projection. *Ero* is characterised by a huge paracymbium that arises from the upper part of the cymbium (Fig. 6B).

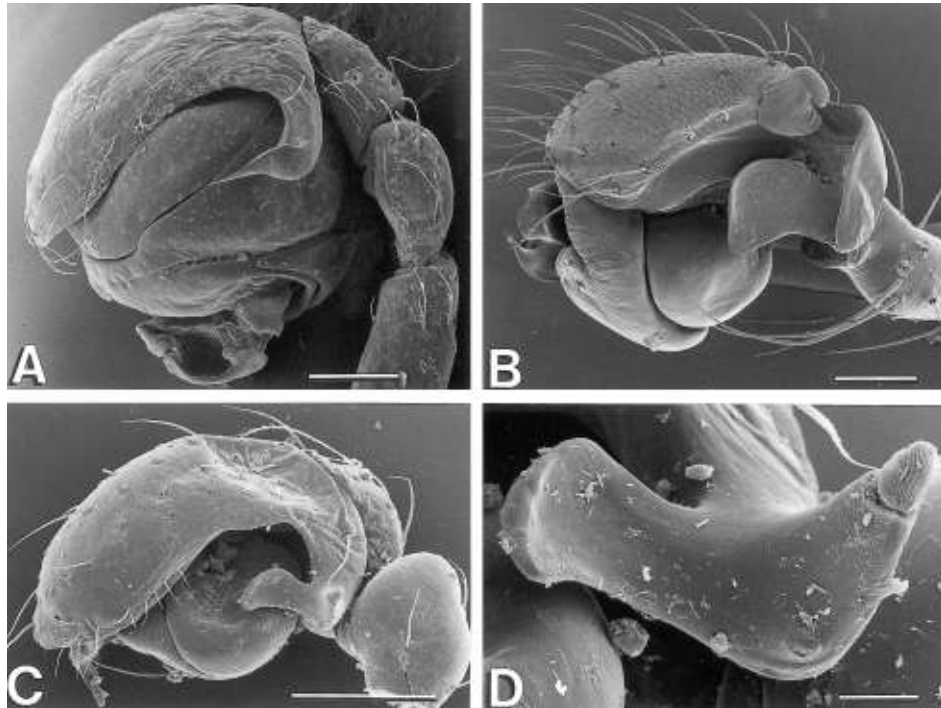
The pedipalps of Anapidae, Micropholcommatidae and Textricellidae are generally simplified, with fewer sclerites and no paracymbial projection in the examined taxa.

### Legs

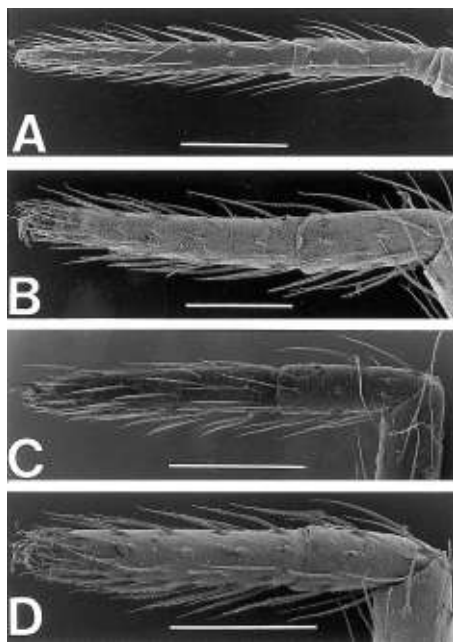
The tarsus is considerably longer than the metatarsus in *?Dippenaaria*, *Pararchaea*, and in the textricellid and micropholcommatid species (Fig. 7A–D). The two apical leg segments are approximately the same length in *Malkara* and *Comaroma*. Only in *Archaea* and *Ero* is the size



**Fig. 5.** Labrum, frontal and lateral view, chelicerae removed. A, B, *?Dippenaaria* sp. (Anapidae), A, male, B, C, female; D, *Parapua punctata* (Micropholcommatidae), female; E, F, *Micropholcomma parmatum* (Micropholcommatidae), E, female, F, male. Scale bars: 10  $\mu$ m.



**Fig. 6.** Male pedipalps with paracymbia of 'palpimanoids' in lateral or dorsolateral (*B*) view. *A*, *Malkara loricata* (Malkaridae); *B*, *Ero cambridgei* (Mimetidae); *C*, *D* *Pararchaea bryophila* (Pararchaeidae). Scale bars: 100 μm.



**Fig. 7.** Tarsus and metatarsus of the fourth (*A–C*) and third (*D*) leg. *A*, *?Dippenaaria* sp. (Anapidae), female; *B*, *Textricella vulgaris* (Textricellidae), female; *C*, *Pararchaea bryophila* (Pararchaeidae), male; *D*, *Micropholcomma parmatum* (Micropholcommatidae), female. Scale bars: 100 μm.

relation typical for most spiders, i.e. the metatarsi are distinctively longer. Simple comparison shows that it is not the tarsi that are elongated, but the metatarsi that have become shorter.

Since the appearance of the tarsal tip varies from leg to leg in a single specimen, it is necessary to use the same leg (here the fourth leg) by way of comparison. All investigated spiders possess a third median claw and, beneath this, accessory setae that are dorsally bent. These setae are plumose in *Archaea*, and serrate at the ventral side in the others (Fig. 8A–D). The fourth tarsal median claw is long and curved in *?Dippenaaria*.

In all studied species the leg cuticle is scaly or squamate (Fig. 8E, F).

The structure of the setae of the legs are difficult to assign to distinct categories and, moreover, a single leg can be covered by more than one type of setae. However, all except *Archaea* are equipped with setae that are clearly serrated (Fig. 8E, F). *Archaea* has plumose hairs only.

No tarsal trichobothria could be observed in any of the species examined. Only the mimetids show a strong ‘spination’ of all legs. Mimetidae and Malkaridae share the feature of prominent macrosetae on the first two pairs of legs. But while the macrosetae in *Ero* form a row on both the metatarsi and tibiae of long curved setae interspersed with 2–5 short curved ones (Fig. 8H), *Malkara* has only 5 equally strongly developed setae on the metatarsi, whereas the setae on the tibiae and tarsi are considerably finer (Fig. 8G). Sexual dimorphism of these macrosetae occurs only in *Ero*, where the male spines are weaker, but not in *Malkara*.

*Pararchaea* has an extremely long trichobothrium apically on the fourth tibia.

*Archaea* is remarkable for its basal thickening of the femora, which is covered with pores.

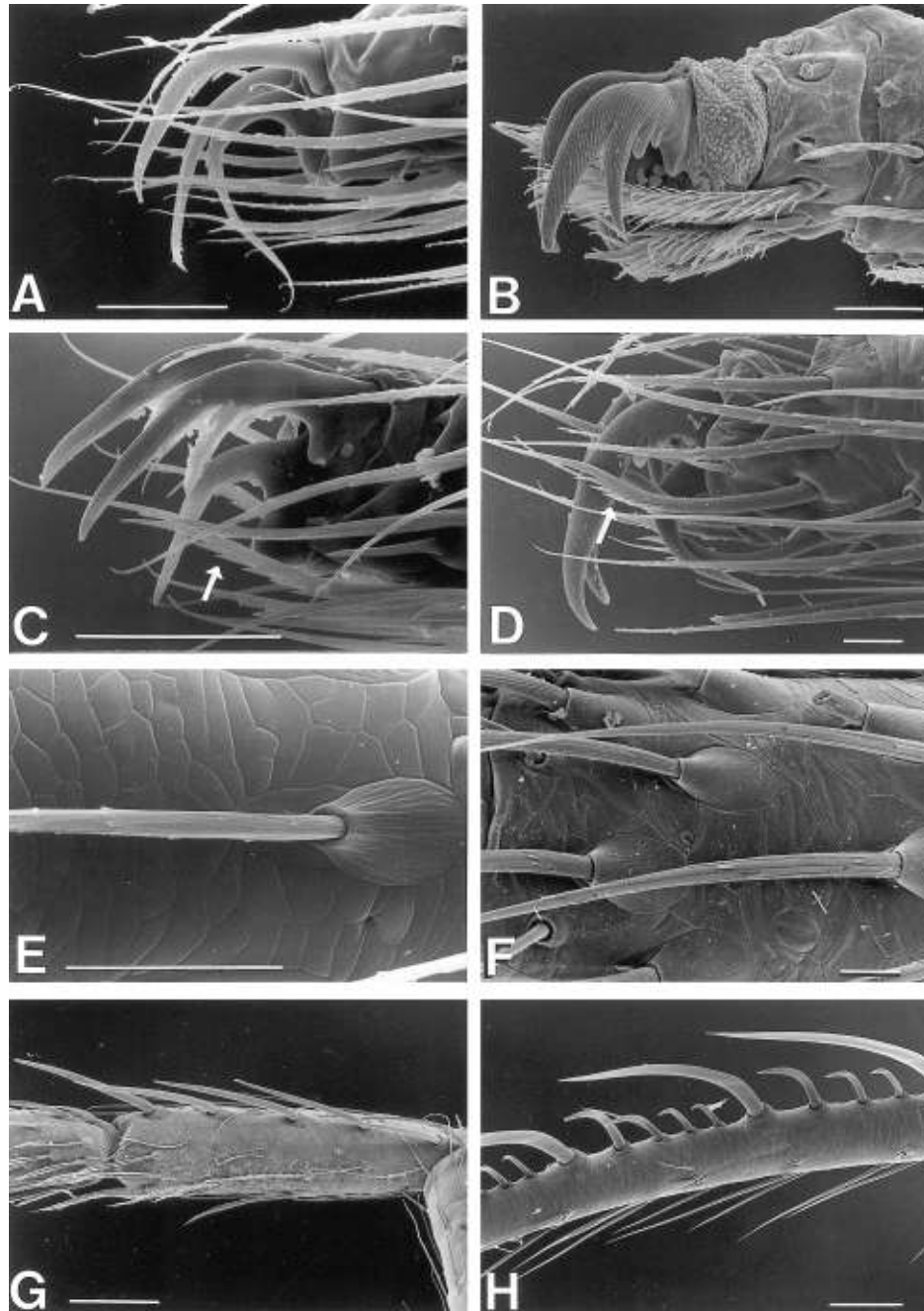
### Spinnerets

A triad is a combination of two aggregate glands and one flagelliform gland located on the posterior lateral spinnerets (PLS). A completely developed triad is present in both sexes in all eight examined species of Anapidae, Micropholcommatidae and Textricellidae (Fig. 9). Its spigots are always located near the distal end of the PLS. *Comaroma simoni* (Anapidae) and *Textricella vulgaris* (Textricellidae) differ from the other species in having both a peculiarly curved shaft in the flagelliform gland spigot (Fig. 9C, D), a feature present in all examined specimens of these two species, but not in any of the other anapids and textricellids. The triad of micropholcommatids is characterised by three more or less equally slender shafts (Fig. 9E). *?Dippenaaria* also has slender shafts in the aggregate gland spigots but the spigot of the flagelliform gland spigot is shorter and separated from the aggregate gland spigots by some distance.

Apart from the triad, other features are shared by the three above-mentioned families. The spigot of the basal cylindrical gland on the PLS shows an enlarged base and is separated by a gap from the rest of the PLS (Fig. 9A, B). Only a very few spigots of aciniform glands could be found, one on the posterior median spinneret (PMS) and one or two on the PLS. The minor ampullate gland on the PMS has a posterior position and is not accompanied by a spigot nubbin.

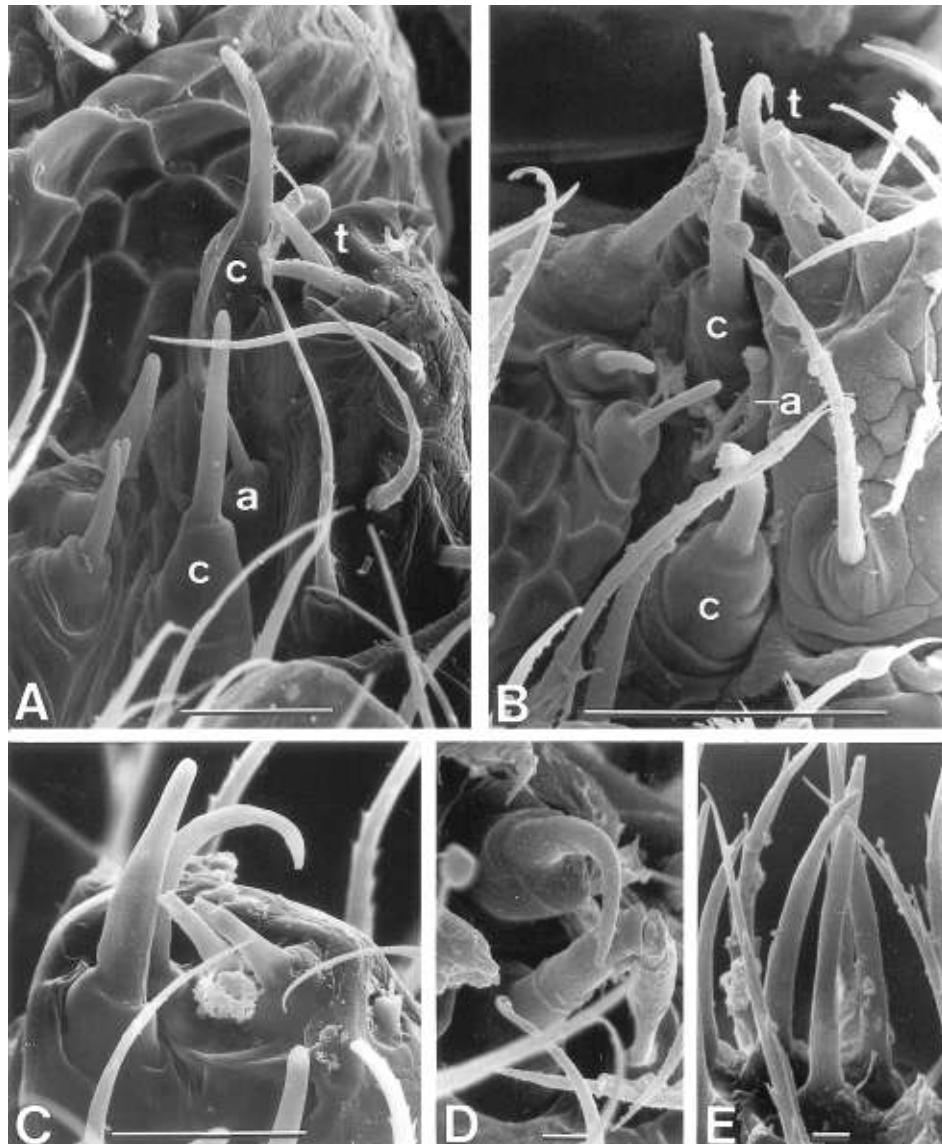
The other four examined spiders (*Ero*, *Malkara*, *Pararchaea* and *Archaea*) lack the triad. No traces of these three-spigot units are detectable in the first instar of an *Ero* species (Fig. 10A). Adult females of *Ero* have only one strikingly enlarged cylindrical gland spigot on each PMS and PLS. These unique spigots have a large circular base, a domed incised shaft and a large opening (Fig. 10B). Up to 13 aciniform gland spigots are present on each PLS, plus 2 on the PMS. The minor ampullate gland spigot is posteriorly located and no spigot nubbin was found.

Examination of the spinnerets of female *Malkara* showed that only the six cylindrical gland spigots are left on the PMS and PLS of both sides. Together they form a transverse row (Fig. 10D). The spigot equipment of the spinnerets is also highly reduced in *Pararchaea* and *Archaea*. The basal cylindrical gland spigot on the PLS is separated off in *Pararchaea* (Fig. 10C) but not in *Archaea*. In both spiders the minor ampullate gland has its spigots on the antero-lateral edge of the PMS.

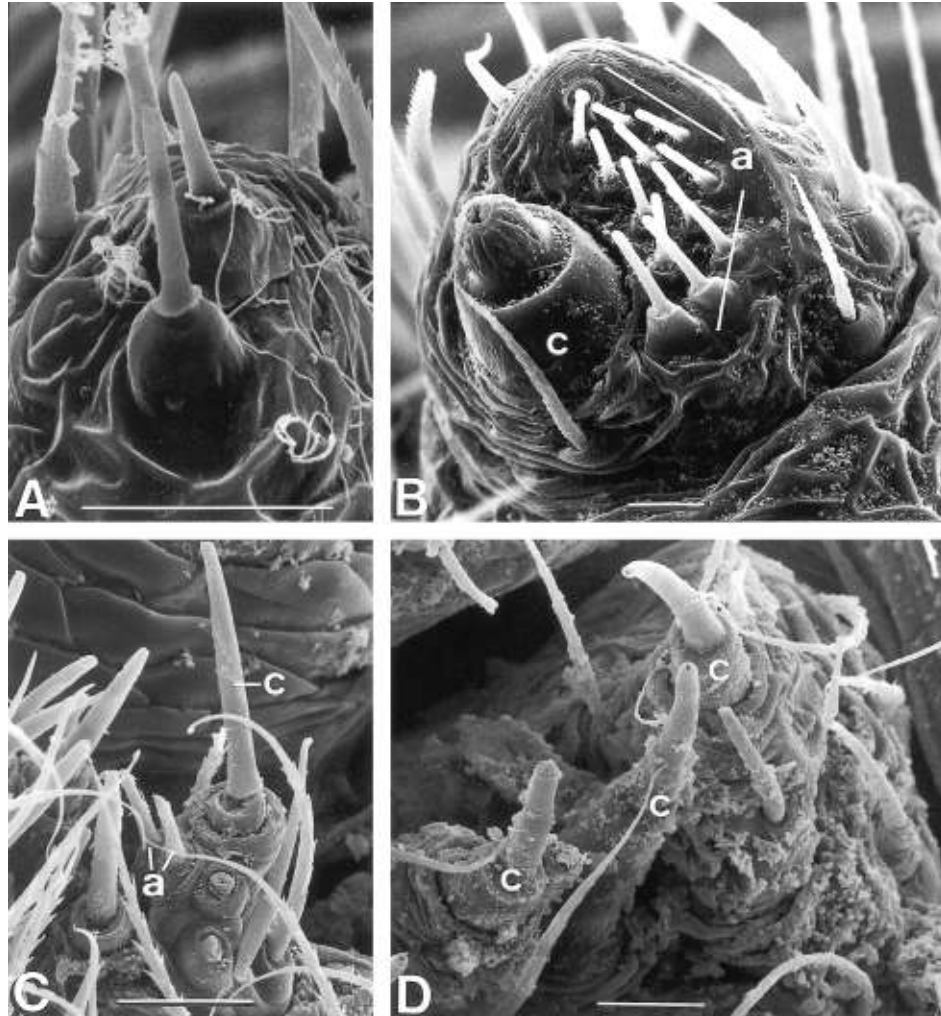


**Fig. 8.** Leg morphology. *A*, ?*Dippenaaria* sp. (Anapidae), female; *B*, *Archaea* (Archaeidae), female; *C*, *E*, *Micropholcomma* sp. (Micropholcommatidae), male; *D*, *F*, *H*, *Ero furcata* (Mimetidae), female; *A*–*D*, tarsal tip of the fourth leg, lateral view; *E*, *F*, cuticle structure and setae of tarsus (*F*) or metatarsus (*E*); *G*, *H*, macrosetae on metatarsus (*G*) and tibia (*H*). Scale bars: *A*–*F*, 10  $\mu$ m; *G*, *H*, 100  $\mu$ m.

Apart from *Archaea*, all spiders included in this study have a distinct colulus that is triangular or linguiform in its outline. The colulus of *Archaea* is very small. *Archaea* differs also from all the other species examined in having no reduced bases in the piriform gland spigots on the anterior lateral spinnerets.



**Fig. 9.** Posterior spinnerets and triads of the left side\*. *A*, *Comaroma simoni* (Anapidae), female, posterior lateral and posterior median spinneret, caudal view; *B*, *Textricella vulgaris* (Textricellidae), female, posterior lateral and posterior median spinneret, caudal view; *C*, *Comaroma simoni* (Anapidae), female, triad and spigot of the cylindrical gland, medio-caudal view; *D*, *Textricella vulgaris* (Textricellidae), female, triad, medial view; *E*, *Micropholcomma* sp. (Micropholcommatidae), male, triad, medial view. Scale bars: *A*, *B*, 10  $\mu$ m; *C*–*E*, 5  $\mu$ m. \**B* shows mirror image of the right side. Abbreviations: a, aciniform gland spigot; c, cylindrical gland spigot; t, triad.



**Fig. 10.** Posterior spinnerets of the left side\*. *A*, *Ero* sp. (Mimetidae), first instar, posterior lateral spinneret, medial view; *B*, *Ero cambridgei* (Mimetidae), female, posterior lateral spinnerets, medial view; *C*, *Pararchaea bryophila* (Pararchaeidae), female, posterior lateral and posterior median spinnerets, medial view; *D*, *Malkara loricata* (Malkaridae), female, posterior lateral and posterior median spinneret, caudo-median view; \**B*, *D* shows mirror image of the right side. Scale bars: 10  $\mu$ m. Abbreviations: a, aciniform gland spigot; c, cylindrical gland spigot.

## Discussion

Only two autapomorphies were proposed to justify the enlarged Palpimanoidea (Forster and Platnick 1984) – cheliceral peg teeth and cheliceral glands opening on elevated mounds. The occurrence of peg teeth in some thomisid and scytodid genera were interpreted as convergent developments, and the lack of peg teeth in Stenochilidae (now included in Palpimanidae) and Holarchaeidae were regarded as a secondary and independent loss (Forster and Platnick 1984). However, distinct cheliceral peg teeth are also lacking in *Malkara*, *Micropholcomma*, *Parapua*

and *Textricella*. Their chelicerae show both true teeth and strong setae with short shafts (Fig. 4D–F). In some cases the strong setae resemble peg teeth to a certain degree, in other cases they are more like setae than teeth. These stiff cheliceral setae show exactly the same appearance as in the Symphytognathidae (Platnick and Shadab 1993). Two conclusions are possible: the above-mentioned taxa have no peg teeth or peg teeth occur also in an araneoid taxon.

Pores on the cheliceral surface that are thought to be of glandular origin occur (as far as is known) in all spiders and were proposed as an autapomorphy of the order Araneae by Selden *et al.* (1991). Thus, only the mound that bears the pores is the actual character. A cheliceral gland mound is present in some male Mygalomorphae (Raven 1986), but was not regarded as homologous with the gland mounds in Araneomorphae. Distinct cheliceral gland mounds are absent in Mimetidae, *Malkara* and *Pararchaea*. In the Textricellidae the pore-bearing mound is fused on the posterior side of each median true tooth, just as in the Anapidae (Fig. 4H).

Both suggested autapomorphies can therefore be seen to be unreliable, so the monophyly of the enlarged Palpimanoidea is poorly justified. A far better supported monophylum is the superfamily Araneoidea: the most important autapomorphic character is the triad and with it the capability of producing gluey capture threads (Coddington 1986).

Even though Platnick and Shadab (1978) and Forster and Platnick (1984) stated that the triad was absent in the Micropholcommatidae and the Textricellidae, it was found in both sexes of all six species of these families examined in this study. The triad of *Comaroma* and *Textricella vulgaris* show striking similarities, whereas the triads of the Micropholcommatidae resemble the linyphiid pattern.

Since the Mimetidae, Malkaridae and Archaeidae *s.l.* are highly specialised predators, often of other spiders and always without a web of their own, the lack of the triad in these taxa can easily be associated with the abandonment of web construction. Even the first instar of *Ero* (Mimetidae) shows no remnant of triad spigots, in contrast to, for instance, the araneoid genus *Pachygnatha* (Platnick *et al.* 1991), but juvenile *Pachygnatha* still spin an orb web (Martin 1978).

The paracymbium of the male palp is another autapomorphy that is always mentioned when the limits and monophyly of the Araneoidea are discussed. This genital feature is much more disputed than the triad because it is difficult to establish homologies of the palpal sclerites (Shear 1981; Coddington 1990a; Hormiga *et al.* 1995). A paracymbium is clearly developed in *Malkara*, *Pararchaea* and the Mimetidae, but not in the other taxa examined. Micropholcommatidae and Textricellidae generally show simplified copulatory organs. Male pedipalps with a reduced number of sclerites and without a paracymbial projection are also typical for the group Anapidae, Mysmenidae and Symphytognathidae. These are regarded as secondary losses (Griswold *et al.* 1998).

The ultrastructure of both the cuticle and setae are an important character complex in higher-level systematics of spiders, though it is difficult to divide the features into distinct categories. However, the leg surface of all examined taxa show the squamate cuticle structure that is typical of araneoid spiders (Lehtinen 1975). All but *Archaea*, which has plumose hairs, are covered with serrate setae. Moreover, another feature shared with the Araneoidea is also present (again with the exception of *Archaea*) in that the accessory setae at the tip of the tarsi are bent upwards, strongly serrated and are used together with the median claw to secure a grip on the threads.

The fact that, on the one hand, most of the examined web-less spiders (still) have legs of the same structure as those of web-building spiders, but, on the other hand, their spinning apparatus is considerably reduced, can be explained by their web-invading behaviour and aggressive mimicry, as has been documented for mimetids by Jackson and Whitehouse (1986).

Griswold *et al.* (1998) established the 'reduced piriform clade' that includes all Araneoidea except the more primitive Araneidae and Tetragnathidae. This new clade is characterised by a piriform spigot base that is reduced or even absent, a character not known from any other group of spiders. With the only exception of *Archaea*, all examined spiders show reduced piriform spigot bases and therefore correspond with the more derived Araneoidea.

The Symphytognathidae was established by Hickman (1931). Several taxa were included that are currently in the families Anapidae, Mysmenidae and Symphytognathidae *s.str.* The monophyly of this group was supported by Forster and Platnick (1977), Coddington (1986), Wunderlich (1986), who correctly named it Anapidae *s.l.*, and Griswold *et al.* (1998). Forster (1959) expanded the Symphytognathidae by including the Micropholcommatidae and the Tetracellidae. Forster's revision was doubted and disputed by Brignoli (1970) and Lehtinen (1975), who argued that the whole taxon was based solely on negative characters, which could simply be caused by size reduction. However, comparisons with very tiny species of the Linyphiidae and the Theridiidae suggests that a simplification of morphological structures is not necessarily associated with minute size. Tiny members of these two families are never lungless, they are only exceptionally covered with abdominal scutae, their eyes and female pedipalpi show no tendencies towards reduction, and their copulatory organs are among the most complex in spiders. In some cases their tarsi are longer than the metatarsi (Brignoli 1970), but this is never as distinct as in the Symphytognathidae *sensu* Forster (1959).

Moreover, the enlarged Symphytognathidae can also be justified by positive characters. The similarities of the cheliceral and spinneret morphology apart (see above), both the Micropholcommatidae and the Anapidae typically show modifications of the first legs in males. These two families share another character: the presence of a labral spur (fig. 5). The term 'spur' is misleading, as it is simply an outwardly curved sclerite on the frontal surface of the labrum that projects towards the chelicerae (Kropf 1990a). The labral sclerite was first mentioned by Wunderlich (1976), erroneously assigned to the labium, and regarded as the characteristic autapomorphy for the Anapidae by Platnick and Shadab (1978), who maintained that it is absent in the Micropholcommatidae and the Tetracellidae. Consequently, *Teutoniella* and *Olgania* were transferred from the Anapidae to the Micropholcommatidae *s.l.* due to the lack of a labral spur (Platnick and Forster 1986, 1989). Platnick and Forster (1986) assumed a second autapomorphy for the Anapidae, a pore-bearing circular depression on the lateral margin of the carapace, but this is not characteristic of all anapids.

Thus, the Anapidae as currently defined, seem to be a paraphyletic group. In this context it is worth mentioning that most but not all anapids spin horizontal orb-webs. Exceptions are, for example, *Comaroma simoni* that weaves a three-dimensional, irregular web (Kropf 1990b) similar to that of *Micropholcomma* (Forster 1959). An extremely derived orb web was described by Shinkai and Shinkai (1988) for the anapid *Conoculus lyugadinus*, whereas *Tetracella* are known to weave little sheets (Hickman 1945). Our knowledge of the web-building behaviour of all these spiders is fragmentary. However, the Symphytognathidae *sensu* Forster should be re-established and a cladistic analysis of this group is urgently needed, because it certainly is more than a 'polyphyletic dump heap of minute araneoid spiders' (Lehtinen 1975).

The Mimetidae, Malkaridae and Archaeidae *s.l.* were excluded from the Araneoidea due to the lack of characters that are associated with web-building behaviour. But the widespread araneophagy in these families is a functional constraint that can conceal polyphyly rather than 'corroborate monophyly' (Coddington and Levi 1991). On the basis of genital morphology, cuticle and setae structure, eye position, labium form, as well as general appearances, it seems justified to assign the Mimetidae and the Malkaridae to the Araneoidea, although their relationships to the other families is currently uncertain. However, some morphological features point to a closer relationship with the Metinae, because both groups have considerably long chelicerae, the shape of the mimetid paracymbium is similar to that of *Meta* and *Metellina*, and *Diphya* has spines on the first and second legs that resemble the mimetid spination pattern (see the review of *Diphya* by Tanikawa 1995). Since the Mimetidae and the Malkaridae are most probably araneoid, the presence of a paracymbium becomes a symplesiomorphic character and the only unique shared synapomorphy left for these two families is the presence of macrosetae on the first two pairs of legs, a character that is also present in the Metinae.

The Archaeidae *s.l.*, which has been split into the current families Archaeidae, Pararchaeidae, Mecysmauchenidae and Holarchaeidae (Forster and Platnick 1984), are in many respects heterogeneous, not only because they are a mixture of haplogyne and entelegyne taxa, but also

with respect to the araneoid autapomorphies. On the one hand, *Pararchaea* has a paracymbium, a squamate cuticle surface and serrate bristles and, thus, shares three apomorphic characters of the araneoid ground-pattern. Selden (1990) discovered similarities between the Mesozoic araneoid *Cretaraneus* and the Pararchaeidae 'that may or may not be an araneoid family'. *Archaea*, on the other hand, lacks a paracymbium, has plumose setae, and their copulatory organs are generally of a very simple type. So there is no evidence for the placement of *Archaea* in the Araneoidea except that they are connected with *Pararchaea* by their cheliceral features and a carapace prolongation that entirely encircles the cheliceral bases. Possibly, *Archaea* is an extremely derived araneoid clade but on the basis of our present knowledge, the placement of the Archaeidae *s.l.* remains an open question.

With the re-assignment of at least four families to the Araneoidea and the possible relationship with Archaeidae *s.l.*, a new analysis of family relationships within the Araneoidea becomes inevitable. Heimer and Nentwig (1982) included the Mimetidae and Archaeidae in their analysis of araneoid relationships and combined them with the Symphytognathidae and Anapidae in one taxon based on the presence of 'cheliceral spines'. This probably referred to peg teeth, a character too weak to be a peg on which to hang a monophylum. Wunderlich (1986) included the Mimetidae and Malkaridae in his fourth and favoured cladogram of araneoid spiders, although he failed to connect them with any sister-group. Griswold *et al.* (1998) declined to consider the disputed families at all.

The Palpimanoidea are now trimmed back to their original size, comprising the Palpimanidae (including Stenochilidae) and Huttoniidae. With this re-limiting of the superfamily the incorrect taxon name 'Palpimanoidea' is at the same time finally settled. Since both families are haplogyne, the placement of the Palpimanoidea inside the 'Higher Entelegyne' is again put up for debate, but, nevertheless, they ought to be considered if the question of the sister-group of the Araneoidea is discussed. The Palpimanoidea were neither included in the cladogram of the Araneoidea (Coddington 1990a; Griswold *et al.* 1998) nor in those of the Entelegyne (Griswold *et al.* 1999) and the Araneomorphae (Coddington 1990b). Platnick *et al.* (1991) provide the only analysis in which they were not omitted, but that study was carried out with the enlarged Palpimanoidea that still includes the groups that should be transferred to the Araneoidea.

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